



Application of Population Modeling to Evaluate Chronic Toxicity in the Estuarine Amphipod *Leptocheirus plumulosus*

by Todd S. Bridges and Steven Carroll

PURPOSE: This technical note describes an application of matrix population modeling to project the ecological effects of chronic sediment toxicity in the estuarine amphipod *Leptocheirus plumulosus*.

EVALUATING CHRONIC TOXICITY WITH *Leptocheirus plumulosus*: Current laws and regulations governing the discharge of dredged material stress the importance of assessing the potential for chronic (long-term) and sublethal effects resulting from exposure to dredged material. To address this requirement, the Long-Term Effects of Dredging Operations (LEDO) research program has sponsored research to develop chronic toxicity tests to evaluate dredged material. This research has resulted in the development of chronic toxicity tests utilizing the marine polychaete *Neanthes arenaceodentata* (Dillon, Moore, and Bridges 1995; Bridges and Farrar 1997) and the amphipod *Leptocheirus plumulosus* (Emery and Moore 1996; Emery et al. 1997). Currently, the EPA and Corps are finalizing a standard protocol for *Leptocheirus* that incorporates research results from both agencies.

Prior to using chronic toxicity tests as regulatory tools in the dredging program, interpretive guidance for establishing a link between responses in the test endpoints (e.g., statistical reductions in individual survival, growth, or reproduction) and ecological effects must be developed (Dillon 1992). Populations of organisms receive considerable attention as ecological endpoints of societal (e.g., protecting the viability of local fisheries) and regulatory concern. The regulations implementing Section 404(b)(1) of the Clean Water Act (PL 92-500) state that, "The permitting authority shall determine in writing the potential short-term or long-term effects of a proposed discharge of dredged or fill material on the physical, chemical, and biological components of the aquatic environment..." and further that, "Tests...may be required to provide information on the effect of the discharge material on communities or populations of organisms...." Population models offer the means for establishing inferences about the likelihood for effects on populations by projecting effects beyond those measured on individual organisms in a toxicity test (Bridges and Dillon 1993).

USE OF MATRIX POPULATION MODELS: Matrix models have been commonly applied in the field of ecology to describe population dynamics for more than 25 years (Caswell 1989). Specifically, these models are applied for population projection when survival rates and birth rates are thought to depend on age or developmental stage. Using matrix models, the population at any time-step is represented as a vector of age-specific or stage-specific population sizes. Multiplying this vector by the transition matrix yields the population size at the next time-step. This is shown in Equation 1 for a general age-based transition matrix with a total of m age classes:

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$$\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \\ \vdots \\ n_m(t+1) \end{bmatrix} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 & \dots & F_m \\ S_1 & 0 & 0 & 0 & \dots & 0 \\ 0 & S_2 & 0 & 0 & \dots & 0 \\ 0 & 0 & S_3 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & S_{m-1} & S_m \end{bmatrix} \begin{bmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \\ \vdots \\ n_m(t) \end{bmatrix} \quad (1)$$

where $n_i(t)$ refers to the number of individuals in age-class i at time t , F_i represents the fecundity, or birth rate, of individuals in age class i , and S_i refers to the survival rate of individuals in age class i . The width of each age class, except the last (the m^{th} age class), is equal to one time-step. For example, if we use one-week age classes (0-1 weeks, 1-2 weeks, etc.), then multiplication by the transition matrix would represent a change in the population over one week in time. The last age class is known as a composite class, defined as all individuals older than a certain age.

After several applications of the transition matrix, the population approaches a stable age distribution, in which the proportion of individuals in each age class remains constant between successive time-steps. At this point, the population grows (or declines) exponentially at a rate determined by the largest eigen-value of the matrix, as shown in Equation 2:

$$N_t = N_0 \lambda^t \quad (2)$$

In this equation, N_t represents the total population size at time t , and λ (lambda) represents the largest eigen-value of the transition matrix. Lambda, also referred to as the finite rate of increase, is generally considered an appropriate summary statistic from which to infer the relative status of a population. At the stable age distribution, if lambda is greater than one, the population will increase exponentially, whereas if lambda is less than one, the population will experience exponential decline to extinction. The major criticism of the use of lambda as a measure of population growth is that natural populations are rarely observed to be at the stable age distribution for a measured transition matrix. This is often due to the fact that survival rates and fecundities in the matrix do not remain constant through time. However, relative values of lambda and the change in lambda can be very useful in summarizing the effects of a particular factor on population growth.

EFFECTS ON LAMBDA: The change in lambda is defined for any pair of treatments, one treatment being designated as the control and the other as the experimental. The change in lambda is simply defined as lambda measured under experimental conditions minus lambda measured under control conditions, or

$$\Delta\lambda = \lambda^e - \lambda^c \quad (3)$$

If the change in lambda is negative, then the change in the varying factor (in this case either sediment concentration or food ration, or both) can be considered detrimental to the population, whereas a positive change in lambda indicates a beneficial influence.

DECOMPOSITION OF THE CHANGE IN LAMBDA: A change in lambda is the direct consequence of changes in vital rates (fecundity and survival rates). Changes in some vital rates do not significantly affect lambda, whereas changes in other vital rates may have a large effect on lambda. One can discern which vital rates have the largest influence on lambda by using Equation 4 (Caswell 1989):

$$\lambda^e - \lambda^c \approx \sum_{ij} (a_{ij}^e - a_{ij}^c) \frac{\partial \lambda}{\partial a_{ij}} \bigg|_{(A^e + A^c)/2} \quad (4)$$

In this (approximate) equation, a_{ij} refers to the element in the i^{th} row and the j^{th} column of the transition matrix. Each term in the summation is referred to as a contribution by a certain vital rate to the change in lambda. Thus the contribution of a vital rate is the actual change in that vital rate multiplied by the rate of change of lambda with respect to that vital rate, measured at the arithmetic mean of the two matrices. This decomposition is quite intuitive, since the contributions to the change in lambda approximately sum up to the actual change in lambda. The approximation is a relatively accurate descriptor of the actual change in lambda.

As a hypothetical example, assume we are testing whether the adverse effects of one sediment would be greater than another sediment using laboratory data. Furthermore, assume that individuals within the population will be classified into five age classes: 0-1 week, 1-2 weeks, 2-3 weeks, 3-4 weeks, and more than 4 weeks. First, an age-based transition matrix would be calculated for each of the two sediment exposures based on data taken from laboratory experiments. The hypothetical lambda measured following exposure to sediment 1 is 1.08 and following exposure to sediment 2 is 0.99. The change in lambda (designating sediment 1 as the control treatment) is -0.09, so the population is better off in sediment 1. The contributions to the change in lambda resulting from the decomposition analysis are listed in Table 1.

Table 1		
Contributions to Change in Lambda		
Age Class	Contribution to Change in Lambda	
	By Survival	By Fecundity
0-1 week	0	0.02
1-2 weeks	-0.04	-0.01
2-3 weeks	-0.01	-0.02
3-4 weeks	0	-0.01
>4 weeks	-0.01	0
¹ Control = food type 1, Experimental = food type 2.		

From this decomposition, it's evident that the largest negative change in lambda was affected by a change in the survival rate of individuals between 1 and 2 weeks of age. Thus we conclude that effects on early survival had the largest influence on population growth when comparing the two sediments.

APPLICATION TO *Leptocheirus*: Matrix population modeling was applied to *Leptocheirus* using effects data collected following exposure to three dilutions of Black Rock Harbor sediment (BRH) (e.g., Bridges and Farrar (1997)). Toxicity was measured in each of the three dilutions of BRH under two food rations to evaluate nutritional effects on toxicity. Three different BRH concentrations were used (0, 3, and 6 percent BRH) and two levels of food ration were applied (normal food ration, 1x; and double the normal food ration, 2x). Survival and reproductive responses were measured in these six treatments (0 percent-1x, 0 percent-2x, 3 percent-1x, 3 percent-2x, 6 percent-1x, and 6 percent-2x) over a period of 30 weeks (Figure 1). These data were then used to parameterize an age-classified matrix population model for *Leptocheirus*.

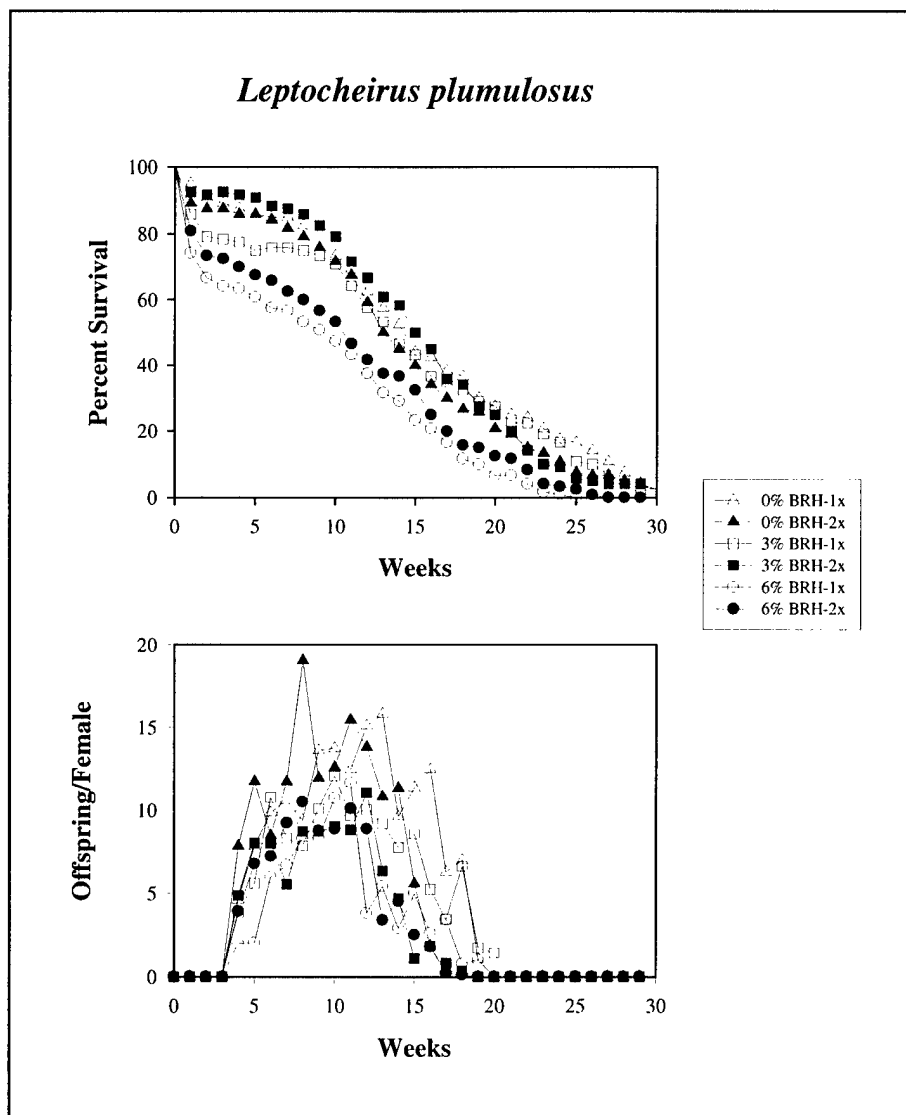


Figure 1. *Leptocheirus* survival and reproduction curves during exposure to BRH

An age-class width of 1 week was used, and 20 age classes were defined. The final age class was a composite class, representing animals 19 weeks of age or older. From the laboratory data, a transition matrix was calculated for each treatment and a lambda was calculated for each matrix. The lambda values are shown in Table 2.

Table 2 Lambda for Each Treatment		
Sediment	Food	
	Normal (1x)	Double (2x)
0%	1.543	1.624
3%	1.472	1.532
6%	1.322	1.397

This table shows that increasing sediment concentration decreased lambda, while increasing food ration increased lambda, as expected. Analysis of variance revealed that effect of sediment concentration on lambda was highly significant ($p < 0.001$), while food ration had a marginally significant effect on lambda ($p = 0.036$), and the interaction between food and sediment was nonsignificant. From this statistical analysis, we can conclude that BRH had a significant adverse effect on the population growth of *Leptocheirus*.

As six different treatments were applied in the lab to *Leptocheirus*, several control/experimental treatment combinations were defined. For each combination, only one of the two factors was varied. The combinations and the change in lambda for each are shown in Table 3.

Table 3 Change in Lambda		
Control	Treatment	Change in Lambda
(0%, 1x)	(3%, 1x)	-0.071
(0%, 2x)	(3%, 2x)	-0.092
(0%, 1x)	(6%, 1x)	-0.221
(0%, 2x)	(6%, 2x)	-0.227
(3%, 1x)	(6%, 1x)	-0.150
(3%, 2x)	(6%, 2x)	-0.135
(0%, 1x)	(0%, 2x)	0.081
(3%, 1x)	(3%, 2x)	0.060
(6%, 1x)	(6%, 2x)	0.075

Table 3 shows that the change in lambda was always in the expected direction: when BRH concentration was increased, lambda decreased, and when food ration was increased, lambda increased. These results would be expected primarily because the sediment was considered toxic and an increase in food ration will cause an increase in the rate of population growth.

DECOMPOSING THE CHANGE IN LAMBDA FOR *Leptocheirus*: As stated earlier, an analysis of variance revealed that sediment had a highly significant effect on lambda ($p < 0.001$), and food had a marginally significant effect on lambda ($p = 0.036$). The next question is whether this change in lambda is due to changes in survival rates, or fecundities, or both, and which vital rates in particular caused lambda to change the most. To address these questions, the change in lambda was decomposed into contributions from the various survival rates and fecundities for each control/treatment combination. For example, consider the combination where the control treatment is 0%-1x, i.e. 0% BRH sediment (control sediment) and normal food ration, and the experimental treatment is 6%-1x, or 6% sediment and normal food ration. Since there was an increase in BRH concentration, but food was held constant, lambda was expected to decrease, which is in fact what occurred: lambda decreased from 1.543 down to 1.322, for a change in lambda of -0.221. Figures 2 and 3 show that the largest (negative) contributions to the change in lambda for this combination came from the survival rate of individuals approximately one week old and the fecundity of individuals approximately five weeks old (both affected a change in lambda of approximately -0.045).

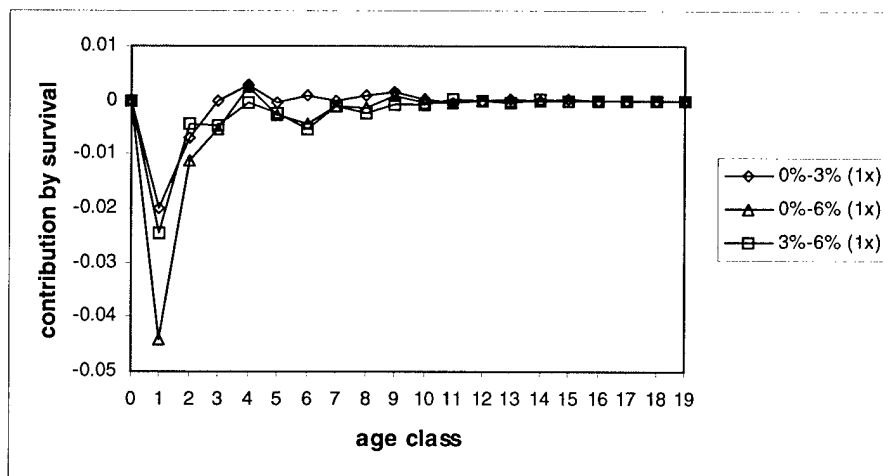


Figure 2. Contributions to the change in lambda by age-specific survival rates for combinations at normal (1x) food ration.

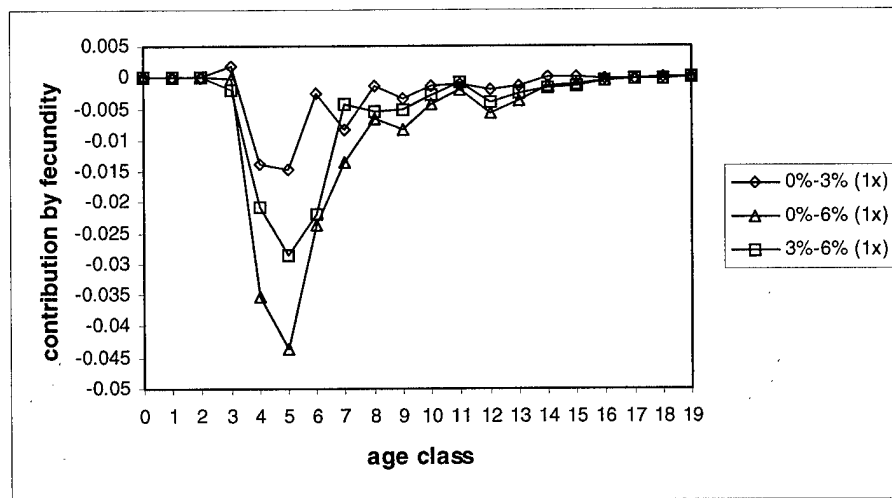


Figure 3. Contributions to the change in lambda by age-specific fecundities for combinations at normal (1x) food ration

SUMMARY OF RESULTS: The largest contributions to the change in lambda for *Leptocheirus* were generally due to changes in survival rates of age classes 1 through 3 and fecundities of age classes 4 through 8. In all cases, the overall change in lambda was in the expected direction; when sediment concentration was increased from control to experimental, lambda decreased; when food was increased from control to experimental, lambda increased. The largest contributions (in the expected direction) were generally statistically significant (statistical significance of contributions was checked by bootstrapping), and several smaller contributions, from older age classes, also proved to be statistically significant.

These experimental results suggest that the 28-day duration of the *Leptocheirus* chronic sediment toxicity test should be sufficient to capture effects on survival and reproduction with the greatest influence on population growth. The decomposition analysis has shown that the main effects on *Leptocheirus* population growth come early in life, through effects on the survival (between one and four weeks old) and reproductive (between four and nine weeks old) rates of young individuals.

RISK APPLICATIONS: The projection matrices calculated in this study can also be used in stochastic models, i.e. models that incorporate random (unpredictable) fluctuations in environmental and demographic factors. Using Monte Carlo techniques, such stochastic models can provide probabilistic estimates of the risk of decline or extinction (Bridges et al. 1996), an approach which more appropriately acknowledges the importance of natural variability and uncertainty in environmental management and decision making. Such a risk-based model for *Leptocheirus* is currently under development by the authors.

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